

VISUAL ECOLOGY OF BITING FLIES

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PERSPECTIVES AND OVERVIEW

Vision has a complex role in the location of resources and mates by insects, and is often integrated with other senses, especially olfaction. Prokopy & Owens (102) reviewed the literature on visual detection of plants by herbivorous insects. A recent increase of interest in the importance of vision in host and resource location by biting flies prompted this review.

Visual ecology may be defined as the description and analysis of an animal's natural optical environment in terms of the animal's visual system and the relationship between environment, visual perception, and behavior (89, 102). This approach is used in our discussion of the visual systems of biting flies. Description of the optical environment entails delineation of parameters such as shape, size, color, contrast, light intensity, and texture. These parameters can be described quantitatively (89, 102) and can be controlled in experiments to discern their importance to insects in their natural environment. Many studies of vision of biting flies have been hampered by insufficient information on the natural habitat or the substrate being tested, or by failure to control the specific orientation behavior being tested; conclusions can often only be inferred.

The photon detection system of Diptera consists of ocelli and compound eyes. Since vision is defined as the ability to detect and utilize patterns of light, our discussion deals primarily with the compound eye, which possesses specialized receptors to detect patterns, movement, contrast, and color. Ocelli primarily detect light versus shaded areas and possibly polarized light; they may be important for entrainment of circadian rhythms (72).

Biting flies display a diversity of activity patterns and are either diurnal, nocturnal, or crepuscular. Species that are crepuscular and nocturnal are unlikely to have well-developed color vision; however, their abilities to detect intensity contrast may be well-developed, enabling them to locate open areas and to discern form and movement. Diurnal species may have well-developed color sensitivity. The importance of vision varies considerably among different biting flies. In a few species, resource location appears to be primarily visual. In many species, visual location of a resource may be only one part of a series of integrated steps. In other species, vision may be only of supplemental importance.

In this review we discuss the present state of knowledge of vision in biting fly behavior and indicate areas that require further research. The review is restricted to the true biting flies; synanthropic flies and immature stages will not be included.

NEMATOCERA

Culicidae

Visual perception of the environment is an important aspect of mosquito behavior in all life stages. Vision, including simple responses to illumination levels as well as the perception of objects, is important in all of the major activities including mating, dispersal, appetitive flight, and the location of sugar sources, hosts, and resting, oviposition, and overwintering sites. Since female mosquitoes feed on blood and then must oviposit, their behavior patterns are more diverse than those of males. The visual ecology of females will be emphasized in this section.

Although controversy surrounds the function of male swarms in mating behavior, there is little question about the importance of vision to swarm formation and maintenance. Swarms commonly form over conspicuous visual markers such as corners of buildings and human observers. Cohesion and horizontal width of the swarm appear to depend on visual characteristics of the swarm marker (49, 97). Males within a swarm apparently respond to each other visually, and females entering a swarm respond visually both to males within the swarm and to the swarm marker (41). Swarming has been observed among nocturnally active, drably colored mosquitoes in Africa (60) and South America (112). Not all mosquito species form swarms. In diurnal forest

species from genera such as *Haemagogus* and *Toxorhynchites* and from the subgenus *Stegomyia* of *Aedes*, mating is associated with hovering behavior. The bright metallic coloration and unique scale patterns of these species may be used in location of conspecifics (60). *Aedes triseriatus* and *Aedes aegypti* occasionally mate in flight in small swarms that form close to host animals, or mate on the hosts themselves (88, 94). Males orient to and grasp conspecific and heterospecific females and other males as they fly; they appear to be responding to moving visual targets (88).

Adult mosquitoes feed on nectar (17, 90), cane sugar (40), extrafloral nectaries, and honeydew (61) in the field. How mosquitoes locate natural sources of sugar remains unknown. Some flowers have ultraviolet-reflecting nectar guides, and many insects utilize these to locate nectar (114). Many Diptera are known to have UV receptors that are sensitive in the 340–360 nm range (120). It is possible that diurnally active mosquitoes use visual patterns, and UV reflectance in particular, to locate flowers in the field. Crepuscular species are less likely to use such cues, owing to the low light levels at dawn and dusk.

Migration, dispersal, and appetitive flight occur at specific times daily and throughout the life of adult mosquitoes. Both visual and nonvisual factors influence these flights. In general, response to light intensity levels initiates flight activity, whereas orientation is controlled by visual perception of the terrain once the mosquito is in flight.

Circadian rhythms have been reported for most mosquito species studied. Crepuscular activity peaks clearly have a physiological basis in monitoring of daily light changes by the mosquito eye (77). Moonlight appears to influence the level of activity of nocturnal species (103). For example, the number of *Aedes taeniorhynchus* collected in Florida was 546% higher during the full moon than on moonless nights (14). Activity of females of all other species sampled increased 122% during the full-moon periods. Light intensity on nights of a full moon is equal to that at twilight, which is when maximum flight activity occurs for many species; the increased light levels from the full moon presumably resulted in increased flight (14).

Extensive field work and laboratory studies (16, 18–20) have shown mosquitoes in flight depend on visual input for orientation. Flight paths of mosquitoes in the field are also affected by vegetative patterns (16). On the basis of their flight preferences, Bidlingmayer (16) grouped mosquitoes as field species, edge species (occurring in ecotones between forests and fields), and woodland species. These groups responded differently to artificial and natural barriers. Field species responded sooner to the barriers, presumably because they were more adapted than woodland species to flying with a horizon in view. These results were further supported by a study in which (a) distant visible objects were attractive to mosquitoes, (b) a change in flight

direction occurred when mosquitoes were in close proximity to visible objects, and (c) woodland species came closer to visible objects than field species (18).

Bidlingmayer & Hem (19) used an elaborate grid system of suction traps to investigate the distance at which various mosquito species respond to visual cues in the field (19). Most species (*Aedes vexans*, *Psorophora columbiae*, *Culex nigripalpus*, and *Culiseta melanura*) responded to suction traps from 15.5–19.0 m. *Uranotaenia sapphirina* and *Culex quinquefasciatus* were found to have visual ranges less than 7.5 m. In another study, woodland species that flew into open areas appeared to maintain visual contact with tall silhouettes, particularly the woodland edge (20). Other authors (27, 52, 53) have also observed the reliance of mosquitoes on visual targets in the field. Giglioli (50) found that in searching flights *Anopheles gambiae* are channelled along visible edges such as the junctions between woodlands and grasslands.

Among the important activities undertaken by adult female mosquitoes are host location and blood-feeding. The detection of movement is important for host location by some species (117). Gillett (51) recounted that field-workers who walked into areas of high mosquito density (particularly *Aedes*) during the daylight hours suspected that their movement was responsible for the initial attraction of host-seeking mosquitoes.

Laboratory studies with artificial targets and anaesthetized hosts (117, 150) and field studies using visual targets in combination with odor (27, 53) have shown the importance of vision in host location. Host-seeking females are generally more attracted to low-intensity colors such as blue, black, and red than to high-intensity colors such as white and yellow (27). Females reportedly exhibit the strongest phototactic responses to blue-green (27) and UV (39). The shape of visual targets also affects attraction (27), and complex patterns appear to attract diurnal mosquitoes (117). Visual cues such as solid dark objects appear to be important to host-seeking nocturnal species (53). The combination of visual stimuli with other cues such as odor, heat, and moisture, however, increases attraction and stimulates landing and initiation of blood-feeding behavior (71).

Mosquitoes must select suitable resting sites each day and must also find sites in which to endure periods of adverse weather and successfully overwinter. The preference of dark surfaces for landing appears to be related to selection of daily resting sites (69). Mosquito species respond to visual characteristics of the terrain according to species-inherent recognition of patterns and illumination levels. Visual images of resting sites within habitats appear to guide the adults toward potential sites (15). Other factors important in selection of sites are temperature and humidity.

Visual factors involved in the selection of suitable hibernation sites are probably similar to those used in the selection of daily resting sites. Overwintering adults generally choose dark, humid, sheltered areas such as caves,

animal burrows, and man-made shelters. The physiological factors leading to hibernation are complex and include response to changing photoperiods (108), which are detected visually.

A gravid female's search for an oviposition site is similar to the host-searching flight in that a variety of cues, including visual ones, are used. The importance of color and of container size and shape has been shown in a number of field and laboratory studies (12, 45, 70, 82, 118). Reflected light from water surface was observed to influence oviposition site location in the field (12) and in the laboratory. Kennedy (80) observed that gravid mosquitoes prepared for oviposition while flying over a mirror. Some gravid mosquitoes respond to the sight of water (95) and movement of larvae (93) at the oviposition site.

The responsiveness of many night-flying insects, including mosquitoes, to artificial lights is considered an aberrant phenomenon. Several theories have been proposed to explain the physiological mechanisms involved (reviewed in 73). Regardless of the mechanisms involved, responsiveness to artificial light (as well as to other visual cues, including motion and contrasting colors) has been exploited in the design of extremely efficient traps for mosquito surveillance (9, 68, 69, 111). Traps have been designed to sample emerging, dispersing, appetitively flying, host-seeking, and ovipositing mosquitoes and have proved invaluable in sampling of pest and vector populations.

Simuliidae

Black flies are for the most part diurnally active (35, 110), with limited activity observed at night (76, 110, 141). Only females feed on blood, and males are not found near hosts; immatures develop in streams and rivers. Most information on the ecology of black flies is derived from field observations and anecdotes.

After emergence during daylight hours, adults move directly to the edge of the river in a flight that is probably visually oriented. Unfed flies show an aversion to highly reflective surfaces such as water, and this aversion may direct the newly emerged flies towards shore (33).

Mating occurs near the emergence site. Two distinct mating strategies have been described (37), and both involve visual orientation. Most commonly, columnar swarms of male flies (144) form over specific visual markers such as shrubs and tree limbs (41). Females are attracted to the swarms, either by visual markers or by the sound of swarming males. Initial contact between the sexes occurs in flight. Orientation of males to females is visual, as shown by experiments in which female mimics elicited mating attempts by males from the swarms (81, 145). A less common strategy entails mating activity on the substrate with little discrimination until body contact is made (116). Males that mate in swarms have more facets in the eye and larger facets in the upper part of the eye than males that mate on substrate. These morphological

adaptations allow swarming males to detect small objects such as females against a bright background of skylight (38, 81).

Black flies use plants as nectar sources, and nectar-feeding flies are usually observed on inconspicuous flowers. It is thought that location of nectar sources is primarily by olfaction (121).

Black flies can be divided into forest species that live near small canopied streams, species that are found in large rivers in open prairies or savannas, and species that are associated with mid-sized rivers and forest clearings and are frequently found at the forest edge (124). It is generally assumed that visual cues for habitat orientation differ among the groups, although there have been few studies. Reliance on visual orientation seems to be greatest among species associated with open terrain and least among forest dwellers (124). Resting at greater vertical heights may result in increased visual detection of movement for forest and edge-dwelling species (41, 124). Long-range migration and short-range dispersal have been documented for many species; however, the role of visual cues in these flights is unknown.

In a comprehensive review, Sutcliffe (121) discussed host location processes in the context of appetitive flight and directed orientation. He discussed long-, middle-, and close-range flight orientation in terms of visual and olfactory cues. Although it is commonly assumed that most black flies embark on appetitive flights actively seeking host cues, there is little evidence to support this. Most research on the role of vision in black flies has been based on close-range orientation. However, vision is thought to be more important in long- and middle-range orientation than current literature indicates. Host location strategies also differ in that many species living in open terrain actively seek hosts, while most forest-dwelling species "passively" locate hosts, often first detecting them from a resting position. The types of visual cues used are assumed to differ between the two strategies.

Information concerning the presence of color receptors is generally inferred from experimental data. Black flies appear to be able to detect UV (115), blue (26), and green (37, 100). Host-seeking flies in the field are most attracted to low-reflectance colors such as blue, black, and red, while white, yellow, and UV-reflective colors are least attractive (23, 26, 36). Strong contrast of traps or hosts against the background is an important factor in the attraction of host-seeking females (23, 26). Thus, low intensity traps placed against highly reflective background vegetation are very attractive (34, 36, 37, 100, 124). Field experiments combining visual traps with odor indicated that flies discriminated traps on the basis of color, independent of the amount of CO₂ (24). Black flies do not exhibit preferences for particular shapes (23, 100). However, increased size of objects increases attraction (7). The importance of host movement to orientation has been examined, but results are equivocal (124, 132).

Many black fly species exhibit specific preferences for feeding sites on hosts and landing sites on traps that may be located by visual cues (13, 141). Some species preferentially land on projecting edges of trap silhouettes (13, 23, 115); this behavior may be related to feeding-site preferences. The very host-specific species *Simulium euryadminiculum* orients toward uropygial gland extracts of loons. However, landing depends on visual stimulus provided by the silhouette of the extended head and neck (13). Simmons (115) observed that flies preferred to land on cow mimics with legs rather than on those without, and he observed species-specific landing preferences that corresponded to behavior on hosts. Preference for the underbelly region is well documented (141) and may be related to the tendency of flies to land on shaded parts of the animal (6, 36). Species that normally feed on cattle (55, 115) sometimes swarm around the heads of humans, but seldom land or bite. When humans assume the quadruped position flies orient to the chest region, but few land (115). General visual and olfactory cues may lead flies to abnormal hosts; however, in the absence of specific landing cues blood-feeding may not occur.

Attraction of host-seeking females to visual stimuli is greatly enhanced when olfactory cues such as CO₂ are added (24, 37, 121, 124). Few flies land on odorless host mimics (100, 124), and those that do are usually campestral species (124). Species such as avian feeders within forests could be collected only in traps baited with CO₂ (43). However, to what extent the traps presented visual cues for orientation is not known.

Black flies can have two types of oviposition behavior; some species drop eggs singly while flying over water, and others lay egg masses on either cobble or trailing vegetation in water (75). Gravid females, in contrast to host-seeking females (36, 115), are attracted to UV-reflecting surfaces (11), which mimic water. Unlike host-seeking females, gravid females of species that oviposit on trailing vegetation are reported to be highly attracted to substrates of high-intensity colors (11) such as yellow and green (37, 100). Choice of oviposition substrate appears to involve more than just visual cues (75).

BRACHYCERA

Tabanidae

Horse flies and deer flies, which are mainly diurnal, belong to the family Tabanidae. Females of this family are hematophagous, although both sexes feed on nectar. Upon emergence or after autogenous gonotrophic cycles, females may make a dispersal flight prior to obtaining blood meals (113). The role of vision in this flight is unknown.

Mating in tabanids generally occurs after the initial in-flight contact of

males and females. In species such as *Tabanus nigrovittatus* (8) and *Chrysops atlanticus* (5), males hover, occasionally darting after other flying insects. If a receptive conspecific is encountered, mating occurs. In other species such as *Chrysops fuliginosus*, males rest on vegetation and dart after passing females (29). Initial detection of females by males is visual, as determined by the fact that males pursued small objects such as stones thrown near them. The importance of vision to this behavior in tabanids is not as well studied as in male bibionids, which behave similarly and have complex visual specializations and flight behavior (151).

Both sexes of tabanids feed on a wide variety of nectar and pollen sources, ranging from grasses to oak trees (91, 148). Nectar is considered a major source of energy for tabanids, yet little is known about their mechanisms for locating nectar sources.

On the basis of electrophysiological and behavioral techniques, blue and green photoreceptors have been detected in *Tabanus bromius* (480 nm and 515 nm, respectively) and *Hybomitra schineri* (487 nm and 528 nm, respectively) (92). Spectral sensitivity curves for *T. nigrovittatus* indicate the presence of photopigments maximally sensitive to UV (350 nm), blue (477 nm), and green (520 nm) (2). Spectral sensitivity curves of males have a higher proportion of blue photoreceptors than those of females, and also differ in having decreasing sensitivity with age. Parous and older females are considerably more sensitive than younger nulliparous females (2). Hanec & Bracken (63) reported that adult tabanids were photopositive to light between 380 and 430 nm and between 500 and 550 nm.

There are numerous reports that tabanids are more attracted to dark-colored than to light-colored animals (125) and objects (57, 104). Response of host-seeking tabanids to color, as determined from field experiments with traps, is generally greatest to blue, red, and black, and for some species, white (21, 26, 57). Green, silver, yellow, and generally white are much less attractive (21, 57). Attraction or lack of attraction to certain hues is independent of intensity of background (3).

Host-seeking tabanids are strongly attracted to solid dark objects, and they have been used in a wide variety of visual traps (21, 22, 126, 128). Information about the factors important in visual orientation of flies to hosts has been largely derived from experimental modifications of visual traps and decoys. Attraction to traps increases as trap size increases (22, 127, 128), possibly owing to the greater visibility of larger objects from a distance. Three-dimensional decoys were more attractive than two-dimensional decoys (21, 129) as a result of their visibility from a greater number of directions and a greater distance. Some host-seeking tabanids are attracted to specific shapes; for example, they may be more attracted to spheres than to vertical or

horizontal cylinders or cubes (21, 129). Others are not attracted to shapes (26). This distinction reflects species-specific differences in host location strategies. Visual attraction decreased when trap surfaces were interrupted by patterning such as stripes (22, 26, 64), which decreased the distance from which traps could be detected. Simple, strongly contrasting patterns were attractive and could be detected from a distance (2). Reports on the importance of movement in attraction of host-seeking tabanids are contradictory (21, 22, 26); more research is needed to clarify this.

High-intensity contrast of objects or hosts against the background enhances their attractiveness to host-seeking female tabanids. This is true whether the background or object is light or dark (3, 21, 104). In a field study on *T. nigrovittatus*, two-dimensional panels with the greatest contrast against the background, regardless of whether object or background was darker, collected the most flies, possibly because they were detected from a greater distance (4). A hue capable of eliciting attraction (i.e. blue) could do so independently of intensity (4). Color contrast is also an important factor in visual attraction. According to Hailman (62), the maximum contrast against a background of grass would be provided by a dark, saturated blue. Host-seeking *T. nigrovittatus*, which are visually sensitive to both blue and green, are strongly attracted to blue traps against a highly reflective background of salt marsh grass (4).

Attraction of host-seeking tabanids to visual traps increases if CO₂ is used as an odor source (113, 126). The level of attraction to visual traps without a CO₂ source varies among species; usually a combination of visual (dark-light contrast) and olfactory (CO₂) stimuli are necessary. *Chrysops* are readily collected in traps with animal baits or CO₂ (149), but are not collected in unbaited stationary traps (64). Attraction to stationary traps is considered the result of active searching behavior, and *Chrysops* spp., which spend much of their time resting, are generally more attracted to traps that emit odor, which elicits flight activity and then visual orientation.

Some tabanid species exhibit preferences for specific feeding sites on hosts (96, 125). Orientation to CO₂ emissions may explain feeding preferences near the head (96); however, the location of other feeding sites may involve visual cues. For example, *T. nigrovittatus* feeds on the undersides of cattle and is commonly trapped in box traps (Manning traps) (2, 64) that provide only visual stimuli and require flies to fly under the trap and then upward through a screen funnel.

Tabanids are reported to oviposit on grass (56), vegetation overhanging water, rocks, or other objects in aquatic environments (130). Visual factors found to be important for attraction of *Chrysops* spp. are the proximity of plants to water (130) and color of oviposition substrate (105). In general,

however, little is known about the importance of vision in location of oviposition sites or substrates.

CYCLORRHAPHA

Muscidae

STOMOXYS SPP. The stable fly, *Stomoxys calcitrans*, is an economically important diurnal species. Both sexes feed on blood. Flies require blood meals about once every 24 hr and are found in close proximity to host aggregations.

Spectral sensitivity curves for adult flies indicate a peak of sensitivity at 360 nm (UV), a broader peak at 450–550 nm (blue-green), and a plateau at 625 nm (orange-red) (1). Both sexes exhibit strong phototactic responses to light in the UV and blue portions of the spectrum (123, 140), which indicates that the flies not only perceive but are also attracted to these wavelengths. Other portions of the spectrum were not found to attract flies.

Both sexes assemble and rest on light-colored objects and surfaces in the vicinity of hosts. Males occasionally dart out from their resting sites at passing flies in attempts to locate a mate (28). Adhesive-coated fiberglass panels are highly attractive to flies in the field (147). The most attractive fiberglass, Alsynite®, displayed substantial reflectance (5–20%) of UV in the range of 300–420 nm. Attractiveness of panels decreased when UV reflectance was decreased by either weathering of the panel or application of sticky adhesives (1).

Assembly of stable flies on surfaces with UV-reflecting properties was related to mating behavior and thermoregulation behavior in cool weather. Flies that rested in the sun on white (UV-reflecting) surfaces at low ambient temperatures (~6°C) increased their internal body temperature to 22–28°C; this permitted them to remain active at relatively low temperatures. When fly body temperatures reached 31–34°C flies were found primarily in shaded resting areas (28). Further support for the role of UV-reflecting surfaces in fly thermoregulation was provided by the observation that attraction to Alsynite® panels increased during cool periods (1).

CO₂ and other host emissions are important cues for host location (48). These cues, in combination with hunger, increase random flight activity, thus increasing the probability that flies will encounter visual cues that they can use to locate hosts (142, 143). High contrast against a background is important in the detection and subsequent orientation of flies to objects or hosts (84, 101). Both sexes of host-seeking flies are more attracted to low-intensity than to high-intensity colors (48, 84, 101). When low-intensity colors are used in traps, collections are increased by the addition of olfactory cues (142, 143).

HAEMATOBIA SPP. The horn fly, *Haematobia irritans irritans*, is an economically important livestock pest. Both sexes blood-feed and are continually associated with their hosts. Horn flies are photopositive to light in the near UV and blue portions of the spectrum (1), and are attracted to UV light traps (65). Spectral sensitivity studies indicate a peak of sensitivity at 360 nm (UV) and a broad peak at 460 nm (blue) (1). There have been a few reports of higher numbers of flies on dark cattle and dark areas of cattle (99). Otherwise, little is known about the role of vision in host orientation; it may be of only minor importance in this diurnal, host-associated species.

Glossinidae

Vision is critical in the biology of tsetse. Spontaneous activity of tsetse, although low, generally follows a diurnal trend, increasing after sunrise, decreasing during mid-day owing to high temperatures, and then increasing again until sunset (25). Starvation increases activity levels (25). The visual responsiveness of females parallels the level of spontaneous activity and is minimal just prior to and during larviposition (79).

Tsetse tend to have a strong photopositive response, which switches to a photonegative response when ambient temperatures exceed 30°C. Prior to larviposition, females become strongly photonegative and tend to rest in dark sites. Immediately after larviposition, they become strongly photopositive regardless of temperature (106).

Tsetse visually choose well-defined resting sites such as woody parts of vegetation (trunks, branches, logs, twigs) and undergrowth, and they appear to spend all but 15–30 min of the day resting (30). The preference of unmated females (107) and males (131) in the laboratory for vertical surfaces and borders of visual contrast is believed to be related to innate alighting and resting behavior. Pregnant females, however, showed strong preferences in the laboratory for landing on horizontal surfaces, simple and unbroken areas, and subterranean cavities (106, 107). This is congruent with larviposition observed in the field, which occurred in shaded areas. Pregnant females show no preference for substrates of particular color in the laboratory (106).

Spectral efficiency curves of *Glossina morsitans morsitans* indicate a peak of sensitivity in the UV (350–365 nm) and a broad peak at 450–550 nm (blue-green). An additional shoulder is also observed at 600–625 nm (orange-red) (59), but this does not necessarily indicate the presence of a related photopigment (146). Major differences in sensitivity of flies of different sexes or ages were not observed. As is typical with diurnal, fast-flying insects, *G. m. morsitans* has a high flicker fusion (131), which confers an ability to detect image movement. Tsetse exhibited strong positive responses to UV light and moderate responses to blue. No photopositive response was seen to green

light (59). Green (58) concluded that *G. m. morsitans* has red-green discrimination ability.

The color most attractive to host-seeking tsetse is blue (31, 78, 122), followed by black (10, 42, 137) and white (42). Yellow and green are consistently unattractive. The relative attractiveness of black, blue, and white depend on the species, the type of trap, and the placement of color on the trap (30, 42). Some trap parameters result in landing, whereas others result in attraction but no landing (67, 134, 136).

UV reflectance does not appear to be important in attracting tsetse. Jordon & Green (78) reported that tsetse were most attracted to fluorescent blue and a nonfluorescent white, whereas other fluorescent colors were not as attractive. Of interest, however, are findings that the brightness of white cloth used for traps correlated with the number of insects collected. As the white cloth yellowed, trap collections decreased 90%; when the cloth was painted white, the traps' attractiveness returned (44).

Tsetse are more attracted to uniform black targets than to targets with numerous or complex edges such as stripes or checkerboards (106, 107, 131). Increasing the size of moving or stationary targets increased the alightment response (67, 134). Many tsetse traps mimic the solid dark shape of a host animal (137). The similarity in shape may be of little importance, however; a very effective visual trap, the biconical trap, bears little resemblance to any animal shape. The attractiveness of this trap is the result of its color or intensity contrast against the background (31).

Strong contrast of an object against the background is an important factor in attraction of host-seeking tsetse (32); *G. morsitans* is thought to be more attracted to brightness of contrast than to color (85, 131). Lambrecht (85) and Barrass (10) obtained conflicting results concerning the attractiveness of black and white. However, both authors suggested that the response of the *G. morsitans* flies reflects their sensitivity to contrast, as it is related to their habitat preference for edge vegetation where contrasts are prominent. Tsetse tend to land on black edges of black and white stripes in laboratory studies; this is believed to be related to resting-site preference (131). Although traps may have certain innate attractive attributes (i.e. size, color, shape), contrast against the background is also important. Hosts are generally seen as dark objects in maximum contrast to vegetation (light background).

High sensitivity to contrast (131) permits tsetse to detect distant objects. Detection is heightened as the brightness contrast between an object and the background increases. The range at which a biconical trap could be detected was estimated to be 10–15 m for *Glossina brevipalpis* and 15–20 m for *Glossina pallidipes* (42). *G. pallidipes* and *G. morsitans* detected an ox from less than 30 m (135). Waage (139) has proposed that the striping pattern of

zebras is a defense against biting flies, since it decreases detection of zebras from a distance. He pointed out that zebra species that are not sympatric with tsetse do not have well-defined striping patterns.

Tsetse take flight during the day in response to stimuli such as odor or movement (136), but may also take flight in the absence of such stimuli (25). Flight occurring in the latter case aids in orientation to stationary hosts (136). Snow (119) presented two models for orientation behavior based on the work of Vale (134, 135). The first model describes flying tsetse that encounter an odor, move upwind toward the host, and enter a limited range of visual attraction. The second model describes resting tsetse that are stimulated by host odors to fly upwind and enter the limited range of visual attraction. Stimuli such as size, contrast with background, and movement are important visual components in attraction of flies to moving hosts. Moving hosts are probably located by a combination of visual and olfactory cues, as location by olfaction alone is considered unlikely (133).

The formation of loose swarms of male and female tsetse behind large slow-moving animals or objects is related to location of hosts for both blood-feeding and mating (25, 134). These swarms consist of both food-seeking and non-food-seeking flies; the latter may be present only for mating purposes. Tsetse evidently express the same behavior in mating as in blood-meal searching (119). The visual attraction of males to large dark moving objects is well documented, as is the attraction of females to objects displaying interrupted movement (47). The formation of swarms by tsetse is thought to increase encounters between the sexes (54), which is important since the flies have low population densities. Males locate females visually (74, 86), dart after them, and attempt to grasp them and copulate. Short-range recognition of females also involves sex pheromones (87). The visual responsiveness of males and females to moving stimuli increases with starvation, except in unresponsive pregnant females. Orientation of tsetse to movement is enhanced by host odor (25). Field studies have shown that moving black and white models are less attractive for landing than stationary models (10). Owaga & Challier (98) concluded that flies attracted to traps with rotating screens were not hungry but were seeking mates. Those attracted to stationary traps were mostly hungry and were seeking a blood meal.

Owing to the economic importance of tsetse, considerable effort has been put into the development of convenient, efficient, and cost-effective traps. Because of different trap designs (98, 137), species-specific responses to traps (66, 133), and varying use of odors in conjunction with trap color or type (122), different traps appear to attract different species and different components of the tsetse population. Many of the traps currently in use are stationary and include an odor source (CO_2 , acetone) for long-range attraction combined with visual stimuli for short-range attraction (134).

Other Flies

The visual ecology of biting flies belonging to Ceratopogonidae, Psychodidae, Rhagionidae, Athericidae, Hippoboscidae, Streblidae, and Nycteribiidae has not been well studied. Although vision does not appear to be very important for host location, it may be important for other behaviors (7, 46, 83, 109).

SUMMARY

Many of the similarities in visual ecology between the Nematocera and Brachycera and within the Cyclorrhapha may reflect the evolution of blood-feeding in these groups. In Nematocera and Brachycera, blood-feeding is thought to have evolved from predatory or nectar-feeding behavior (138). Only females feed on hosts, and association with hosts generally occurs when hosts are close to the aquatic or semiaquatic habitats of the immatures. Flies feed on nectar, make appetitive flights, disperse, or migrate prior to blood-feeding, and then oviposit in water. Many species are nocturnal or crepuscular. In Cyclorrhapha, flies are closely associated with hosts. They may have arisen from compost-feeding flies that developed a larval dependence on vertebrate-produced microhabitats. Both sexes blood-feed, and mating occurs on or near hosts. Flies generally emerge in the proximity of hosts and maintain close contact with them. These species are diurnal, and their visual systems are well developed. Comparisons between closely related blood-feeding and non-blood-feeding species may provide insight into the visual ecology of blood-feeding species.

Despite the different origins of hematophagy, there appears to be a convergence of morphology and behavior that is related to ecology rather than to phylogenetic relationships. This is clearly seen in host-location strategies by tsetse and tabanids. Even within groups such as mosquitoes, species that are active at the same time of day and in the same habitat have more in common than closely related species in different habitats. For this reason, an ecological review would be more cohesive than this phylogenetic discussion. However, because of the disproportionate amount of literature on a small number of groups, the phylogenetic approach is the most practical for this subject. However, this review does point out the great need for research on the less well-studied groups and behaviors.

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